

ANTENNARIA ALPINA (ASTERACEAE: INULEAE):
REVISION OF A MISUNDERSTOOD ARCTIC-ALPINE
POLYPLOID SPECIES COMPLEX

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ABSTRACT. Canonical discriminant analysis was used to determine: (1) whether *Antennaria alpina* occurs in North America or not; (2) which character or combination of characters could best be used to distinguish members of the *A. alpina* and *A. media* polyploid complexes; and (3) whether infraspecific taxa warrant formal recognition in *A. alpina*. The results of this investigation indicate that *A. alpina* does occur in North America. The main morphological distinctions between the two aforementioned polyploid complexes are the presence of scarious tips at the ends of middle to distal peduncular leaves in *A. alpina*, these being absent in *A. media*, and the shape of the involucre bracts. The analyses support the recognition of infraspecific taxa in *A. alpina*. To maintain consistency with other recent revisions of polyploid complexes in the genus, the rank of subspecies (*A. alpina* subsp. *alpina*, subsp. *canescens*, and subsp. *porsildii*) was selected. In addition to minor quantitative differences, the three subspecies differ with respect to the degree, distribution, and type of pubescence on the basal leaves.

Key Words: *Antennaria alpina* subsp. *alpina*, *A. alpina* subsp. *canescens*, *A. alpina* subsp. *porsildii*, Asteraceae, Inuleae, polyploid species complex, canonical discriminant analysis

Over the past fifteen years five of the *Antennaria* (L.) Gaertner polyploid species complexes which occur, in whole or in part, in arctic or arctic-alpine North America have been revised. These include *A. neodioica* E. L. Greene (Bayer 1989a; Bayer and Stebbins 1982), *A. rosea* E. L. Greene (Bayer 1989b; Chmielewski and Chinnappa 1988a), *A. monocephala* DC. (Chmielewski and Chinnappa 1991), *A. frieseana* (Trautv.) Ekman (Bayer 1993; Chmielewski 1994a), and *A. media* E. L. Greene (Chmielewski 1997). Only two major North American arctic-alpine polyploid species complexes remain in need of revision, that of *A. alpina* (L.) Gaertner and *A. pulcherrima* (Hook.) E. L. Greene. The former complex, which is the focus of this investigation, has had no less than a dozen infraspecific taxa described in North America alone (Cronquist 1955; Fernald 1924; Rydberg 1917; Scoggan 1979; Welsh 1974). Despite the recognition of these taxa, as well

as the occurrence of *A. alpina s.l.* in Scandinavia and Greenland, some past authorities (Greene 1898; Malte 1934; Porsild 1965) questioned whether this purported circumpolar complex (Ekman 1927) occurred in North America. Disagreement among authors was, and still is in part, attributable to the green-black phyllaries shared by members of both the *A. alpina* and *A. media* polyploid complexes, as well as the fact that members of each complex exhibit a high degree of morphological variability and thus morphological overlap. This variability is due, in part, to polyploidization (Bayer 1984, 1990a; Bayer and Stebbins 1981, 1987; Chinnappa 1986; Chmielewski and Chinnappa 1988b, c, 1990), as well as the extensive geographic ranges over which the complexes extend (Bayer and Stebbins 1987; Chmielewski 1997). Because considerable morphological overlap was believed to exist between the two complexes, Jepson (1925) proposed the recognition of *A. media* as a variety of *A. alpina*. Bayer (1993) and others before him (Fernald 1924; Greene 1898; Rydberg 1900) noted that two characters distinguished *A. alpina* from *A. media*. First, and most importantly, is the presence of flat, scarious tips (flags) at the ends of the middle to distal peduncular leaves (historically referred to as cauline leaves) in the former species, these being mostly absent in the latter. Second, the phyllaries of pistillate *A. alpina* are typically acute, whereas in *A. media* they are blunt. Both complexes were treated as distinct by Bayer and Stebbins (1993) in their synopsis of North American representatives of the genus. In addition, *A. alpina* was recognized by Bayer and Stebbins (1993) as being composed of innumerable apomictic clones; thus they recommended that circumscription should follow a broad species concept, noting that further studies were necessary prior to finalizing treatments for the two complexes.

The objectives of this investigation were to determine: (1) whether *Antennaria alpina* occurs in North America; (2) which, if any, character or combination of characters could best be used to distinguish between members of the *A. alpina* and *A. media* complexes; and (3) whether any infraspecific taxa warrant formal recognition in *A. alpina*.

MATERIALS AND METHODS

Herbarium specimens of *Antennaria alpina s.l.* from Scandinavia and Greenland, presumed *A. alpina* from North America,

and *A. media s.l.* from North America (as defined and utilized in Chmielewski 1997) used in the phenetic study were borrowed from C, CAN, CAS, CM, DAO, DAV, GH, IDS, MONTU, MT, NDG, RENO, RM, S, SD, SLRO, UAC, UBC, US, UT, and WS (Holmgren et al. 1990). Representative specimens of the *A. media* polyploid species complex were cited previously (Chmielewski 1997); representative specimens and types of *A. alpina s.l.* are listed in the Taxonomic Treatment. The taxa and their names adopted at the conclusion of the investigation [*A. alpina* subsp. *alpina*, *A. alpina* subsp. *canescens* (Lange) Chmielewski, and *A. alpina* subsp. *porsildii* (E. Ekman) Chmielewski] will be used throughout the body of the text for the sake of clarity, except when used in reference to previous publications. Specimen selection and identification follow the methodology of Chmielewski (1993). No *a priori* restrictions were placed on the total number of specimens deemed necessary to represent the range of variation within *A. alpina s.l.* Qualitative characters used to identify specimens to species prior to analysis included: habit (presence or absence of stoloniferous growth); the presence or absence of flat, scarious tips (flags) at the ends of the middle to distal peduncular leaves; degree, distribution, and type of pubescence on basal leaves; glandularity, if any; color, shape, and texture of the phyllaries; exertion of the style; and occurrence of papillae on the cypsela (historically referred to as an achene).

Data were collected for 16 quantitative characters. These included the vegetative characters basal leaf length and basal leaf width; the vegetative-reproductive characters peduncle length, number of peduncular leaves, peduncular leaf length, peduncular leaf width, number of capitula, involucre length, outer phyllary length, outer phyllary width, inner phyllary length, and inner phyllary width; and the reproductive characters cypsela length, pappus length, style length, and corolla length. The selection of these characters was based on their usefulness in previous revisions of the genus by this laboratory (Chmielewski 1993, 1994b, 1995a, b, 1996, 1997; Chmielewski and Chinnappa 1988a, 1991; Chmielewski et al. 1990a, b). Only pistillate plants were utilized in the phenetic analysis because inclusion of the few available staminate collections, specifically from *Antennaria media s.l.*, necessitated the exclusion of style length, which was deemed unacceptable. Each data matrix was, therefore, complete for all characters (see Bayer 1992 and Chmielewski and Chinnappa 1992 for

a discussion on the acceptability and use of incomplete data matrices in phenetic studies of *Antennaria*).

Prior to initiating the various statistical procedures, length measurements were transformed to their logarithms (base 10) and count data to their square roots (Cooley and Lohnes 1971; Gilbert 1968). Classificatory discriminant analysis, using the SAS (SAS Institute Inc. 1989) DISCRIM procedure, was first used to classify specimens identified *a priori* to their respective taxonomic group. Several options, including list, simple, pool, spool, cross-validate, crosslist, and posterr were included with this procedure. Correct identification rates (Pimentel 1979; Pimentel and Frey 1978) were used as indicators of separation between or among groups of specimens. The classification criterion was used subsequently to assign additional specimens to one of the previously defined groups. This *a posteriori* assignment of specimens assumes that they do indeed belong to one of the *a priori* groups of specimens and not to a taxonomic group excluded from the study.

Canonical discriminant analysis was used to summarize among-group variation. Bivariate plots of canonical variate scores were used to facilitate visualization of discontinuities between and among groups of specimens (DeltaPoint Inc. 1992). Descriptive statistics reported in the taxonomic treatment were calculated using the SAS UNIVARIATE procedure (SAS Institute Inc. 1989).

Three data matrices were analyzed during the course of the investigation. The first matrix consisted of 371 specimens and initially was used to test whether North American specimens believed to be part of the *Antennaria alpina* polyploid complex ($n = 142$) could be distinguished from North American *A. media s.l.* ($n = 229$). Results based on the analysis of these data would: (1) demonstrate whether the two taxa are morphologically distinct (based on quantitative versus qualitative differences); and (2) define quantitative characters that could best be used to differentiate between members of the two complexes.

The second data matrix consisted of the same 142 specimens of North American *Antennaria alpina* used in the first data matrix and specimens of *A. alpina* from either Greenland ($n = 69$) or Scandinavia ($n = 39$). Results based on the analysis of these data would: (1) demonstrate whether geographic separation correlates with selection for different morphotypes; (2) define quantitative

characters that could best be used to differentiate among individuals from each of the three geographic areas; and (3) possibly provide information on the directionality of postglacial colonization of Greenland by members of the polyploid complex.

The third data matrix included the 250 specimens of data matrix two. These were divided into the following three groups: (1) 182 specimens previously treated as *Antennaria alpina* were treated as *A. alpina* subsp. *canescens*; (2) 18 specimens previously treated as Greenland *A. alpina* were treated as *A. alpina* subsp. *porsildii*; and (3) the remaining 50 specimens were treated as *A. alpina* subsp. *alpina*, regardless of their geographic origin. Type collections of *A. alpina* var. *cana* Fernald & Wiegand (n = 3), *A. alpina* var. *canescens* Lange (n = 1), *A. alpina* var. *glabrata* J. Vahl (n = 1), *A. arenicola* M. O. Malte (n = 1), *A. atriceps* Fernald (n = 2), *A. brevistyla* Fernald (n = 1), *A. canescens* f. *fastigiata* Böcher (n = 1), *A. columnaris* Fernald (n = 3), *A. confusa* Fernald (n = 8), *A. congesta* M. O. Malte (n = 1), *A. glabrata* (J. Vahl) Greene f. *ramosa* A. E. Porsild, *A. longii* Fernald (n = 6), *A. porsildii* E. Ekman (n = 4), *A. sornborgeri* Fernald (n = 1), *A. subcanescens* Ostenfeld ex M. O. Malte (n = 2), and *A. vexillifera* Fernald (n = 3) were used in the *a posteriori* component of the analysis. Specimens of *A. alpina* f. *latifolia* E. Ekman and *A. alpina* var. *ungavensis* Fernald were over-mature (florets had detached from the receptacle) and, because of the missing data, could not be included as part of the *a posteriori* analysis. Results based on analysis of these data were expected to: (1) demonstrate whether the recognition of infraspecific taxa is warranted; (2) define those quantitative characters which could best be used to differentiate among the infraspecific taxa; and (3) facilitate assignment of the respective type collections of unassigned taxa to one of the recognized infraspecific taxa.

RESULTS

Two *a priori* complexes (North American *Antennaria alpina* s.l. and *A. media* s.l.). Evaluation of the discriminant function through the use of cross-validation identification indicated that 83.3% of the 371 specimens utilized were assigned with the highest Geisser assignment probability (mean \pm standard deviation) to the correct *a priori* species complex (*Antennaria alpina* s.l., 86.6%, 0.923 ± 0.110 ; and *A. media* s.l., 81.2%, 0.918 ± 0.122).

Table 1. Summary of Mahalanobis distances between pairs of geographic groups and their associated squared distance F-values (in parentheses).

	Greenland	Scandinavia
North America	2.16 (5.88)	6.02 (10.81)
Greenland		5.23 (7.65)

The Mahalanobis distance between species complexes (3.18) and associated squared distance F-value (16.73) indicate that their respective centroids (-1.10 and 0.68) were significantly different ($P < 0.0001$). The canonical correlation of the first discriminant function (0.66), which squared is the proportion of the total variance explained by the function (0.43), indicates that the recognition of these two complexes explains a low amount of the overall variation. Except for peduncle length, characters with high loadings on the first canonical axis (style length, inner phyllary length, involucre length, and corolla length) were associated with either the capitulum or the floret.

Three *a priori* groups (*Antennaria alpina s.l.* from North America, Greenland, and Scandinavia). Evaluation of the discriminant function through the use of cross-validation identification indicated that 83.6% of the 250 specimens were assigned with the highest Geisser assignment probability (mean \pm standard deviation) to the correct *a priori* geographic group (*Antennaria alpina s.l.* from: North America 78.2%, 0.930 ± 0.115 ; Greenland 87.0%, 0.909 ± 0.114 ; and Scandinavia 97.4%, 0.951 ± 0.107). The Mahalanobis distances between pairs of geographic groups (Table 1) and associated squared distance F-values indicated that all between-geographic group comparisons of centroids (Figure 1) were significantly different ($P < 0.0001$). The first canonical variate accounted for 67.3% of the among-group variation. The canonical correlation coefficients associated with the first two canonical axes (0.65 and 0.52) indicate that the overall goodness of fit between the variables and classification is weak. Characters that had high loadings on the first canonical axis (pappus length, style length, involucre length, inner phyllary length, and corolla length) are associated with either the floret or the capitulum and may best be used to separate the groups of specimens. Characters that had high loadings on the second canonical axis included number of capitula, basal leaf width, and outer phyllary width.

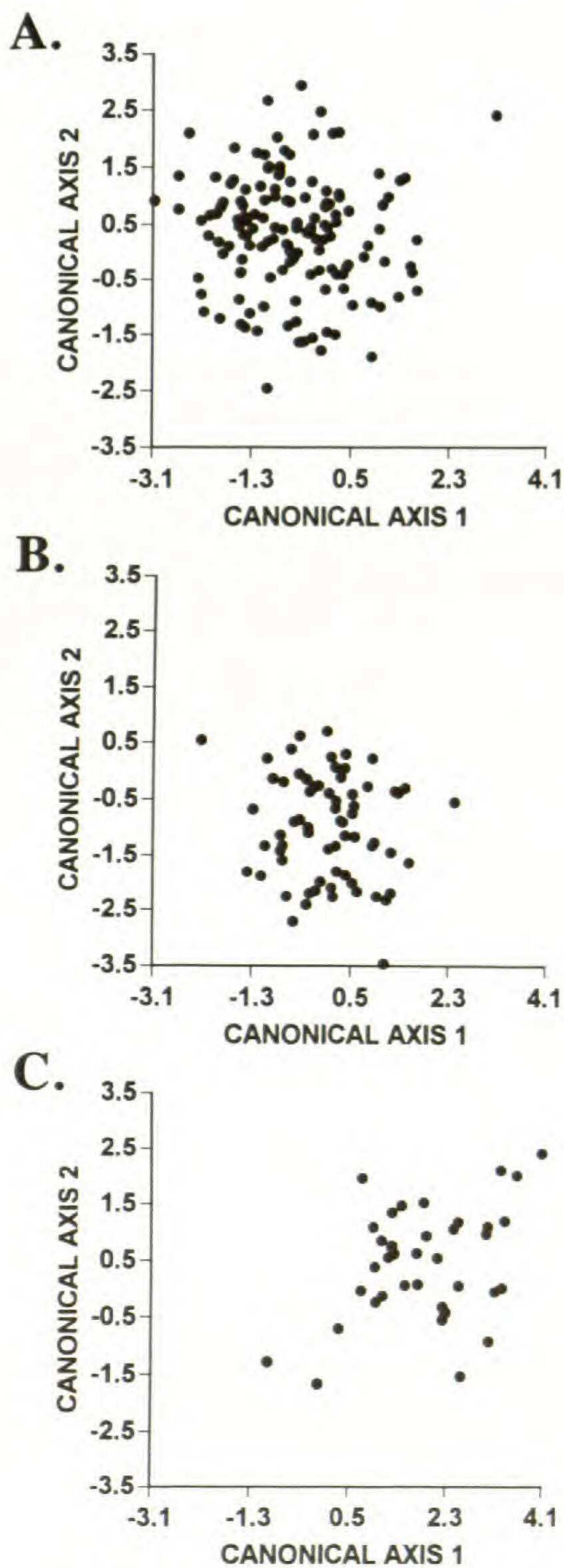


Figure 1. Ordination of canonical variate scores and summary of group centroids for *Antennaria alpina* s.l. from: (A) North America (-0.57, 0.34); (B) Greenland (0.10, -0.97); and (C) Scandinavia (1.88, 0.47).

Table 2. Summary of Mahalanobis distances between pairs of infraspecific taxa and their associated squared distance F-values (in parentheses).

	subsp. <i>canescens</i>	subsp. <i>porsildii</i>
subsp. <i>alpina</i>	4.01 (9.24)	12.57 (9.77)
subsp. <i>canescens</i>		6.43 (6.19)

Three *a priori* groups (*Antennaria alpina* subsp. *alpina*, subsp. *canescens*, and subsp. *porsildii*). Evaluation of the discriminant function through the use of cross-validation identification indicated that 89.6% of the 250 specimens were assigned with the highest Geisser assignment probability (mean \pm standard deviation) to the correct *a priori* infraspecific taxon (*Antennaria alpina* subsp. *alpina*, 96.0%, 0.951 ± 0.098 ; subsp. *canescens*, 86.8%, 0.951 ± 0.103 ; and subsp. *porsildii*, 100%, 0.999 ± 0.000). The Mahalanobis distances between pairs of infraspecific taxa (Table 2) and associated squared distance F-values indicated that all between-infraspecific group comparisons of centroids (Figure 2) were significantly different ($P < 0.0001$). The first canonical variate accounted for 69.3% of the among-group variation. The canonical correlation coefficients associated with the first two canonical axes (0.66 and 0.50) indicate that the overall goodness of fit between the variables and classification is weak. Characters that had high loadings on the first canonical axis included number of peduncular leaves, peduncle length, basal leaf width, number of capitula, and peduncular leaf width. Three characters (number of peduncular leaves, peduncle length, and number of capitula) can best be used to separate subsp. *alpina* and subsp. *canescens* from subsp. *porsildii*. Basal leaf width is only somewhat useful in separating subsp. *alpina* from both subsp. *canescens* and subsp. *porsildii*. Eight characters (outer phyllary length, inner phyllary length, inner phyllary width, outer phyllary width, corolla length, cypsela length, pappus length, and involucre length) had high loading on the second canonical axis. These vegetative-reproductive characters associated with the capitulum and reproductive characters associated with the floret are selectively useful in separating the subspecies. Generally, subsp. *alpina* and subsp. *porsildii* are more similar to each other with respect to these characters than either is to subsp. *canescens*. Therefore, the former five and latter eight characters can best be

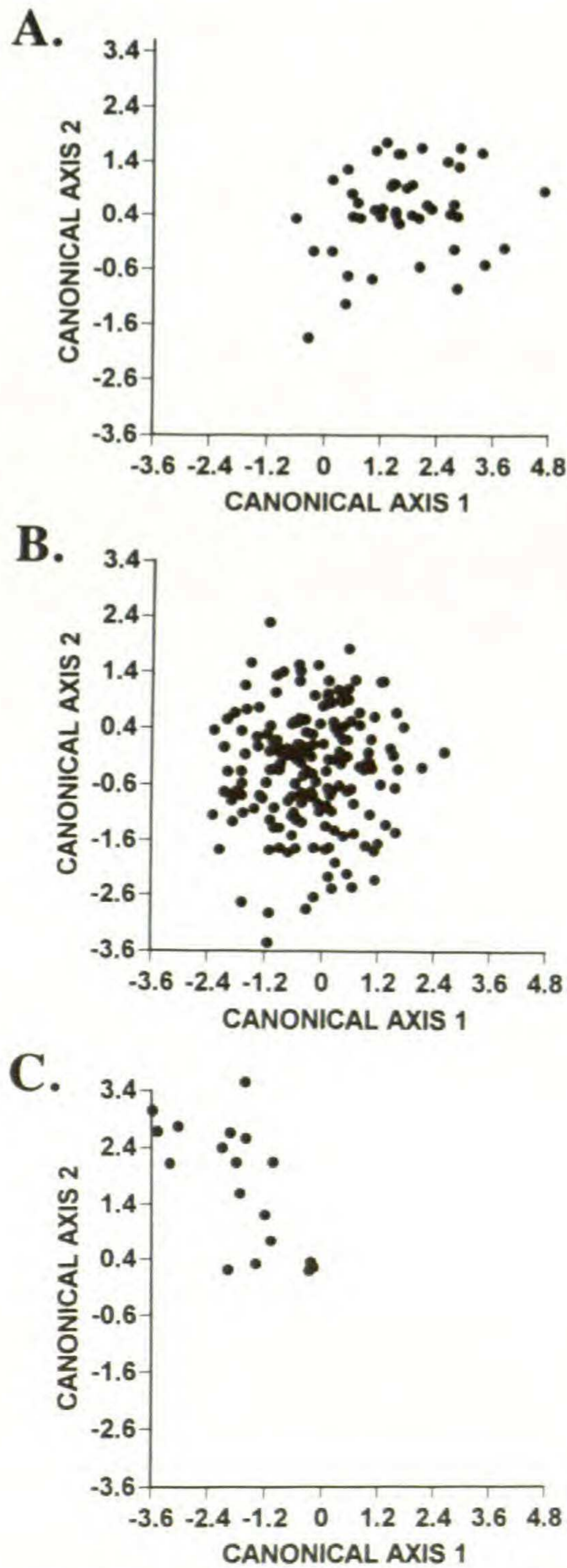


Figure 2. Ordination of canonical variate scores and summary of group centroids for *Antennaria alpina*: (A) subsp. *alpina* (1.57, 0.51); (B) subsp. *canescens* (-0.26, -0.31); and (C) subsp. *porsildii* (-1.76, 1.73).

Table 3. Summary of descriptive statistics (mean \pm standard deviation) for *Antennaria alpina* subsp. *alpina* (n = 50), *A. alpina* subsp. *canescens* (n = 182), and *A. alpina* subsp. *porsildii* (n = 18).

	subsp. <i>alpina</i>	subsp. <i>canescens</i>	subsp. <i>porsildii</i>
Peduncle length (cm)	11.6 \pm 2.9	7.9 \pm 3.0	6.2 \pm 1.9
Number of peduncular leaves	9.2 \pm 1.9	7.4 \pm 1.9	5.9 \pm 1.5
Peduncular leaf length (mm)	14.6 \pm 3.1	11.3 \pm 2.5	11.7 \pm 1.7
Peduncular leaf width (mm)	1.9 \pm 0.5	1.5 \pm 0.4	1.5 \pm 0.3
Basal leaf length (mm)	13.3 \pm 2.7	10.5 \pm 3.1	12.8 \pm 3.4
Basal leaf width (mm)	3.2 \pm 0.7	2.7 \pm 0.7	2.5 \pm 0.5
Number of capitula	5.6 \pm 1.7	4.4 \pm 1.4	2.7 \pm 1.4
Involucre length (mm)	6.3 \pm 0.7	5.8 \pm 0.5	6.2 \pm 0.5
Outer phyllary length (mm)	4.4 \pm 0.7	4.0 \pm 0.6	4.6 \pm 0.6
Outer phyllary width (mm)	1.1 \pm 0.2	1.1 \pm 0.2	1.2 \pm 0.3
Inner phyllary length (mm)	5.7 \pm 0.6	5.3 \pm 0.5	5.9 \pm 0.5
Inner phyllary width (mm)	0.7 \pm 0.1	0.7 \pm 0.2	0.8 \pm 0.1
Cypsela length (mm)	1.2 \pm 0.3	1.1 \pm 0.3	1.1 \pm 0.2
Pappus length (mm)	5.4 \pm 0.5	4.9 \pm 0.4	5.4 \pm 0.4
Style length (mm)	5.0 \pm 0.7	4.4 \pm 0.5	4.7 \pm 0.4
Corolla length (mm)	4.2 \pm 0.5	3.8 \pm 0.4	4.3 \pm 0.5

used in various combinations to differentiate among the three subspecies of *A. alpina* (Table 3).

A posteriori assignments of type collections believed to be included within this polyploid complex are also summarized (Table 4).

The geographic distributions of specimens representing the three subspecies accepted at the conclusion of the study are illustrated in Figures 3–5.

DISCUSSION

Analysis of the first data matrix was intended to address the question of whether *Antennaria alpina* occurs in North America or not. Arguably, one of the major difficulties associated with answering this question is deciphering to which morphological entity previous authors were referring.

Greene (1898) was apparently the first North American author to formally note that *Antennaria alpina* was common in the mountains of Norway and Greenland, but that it was not known to occur on the North American continent. Nelson (1901) concurred. Fernald and Wiegand (1911) opined that further investigation would indicate that the species was circumpolar, and that

many of the described arctic and alpine taxa would better be treated as geographic variants or infraspecific taxa of *A. alpina*. Holm (1920) noted that it would "seem very unnatural" for the circumpolar *A. alpina* not to occur on the North American continent, as it is frequent in Greenland. Fernald (1924) asserted that typical *A. alpina* (*A. alpina* var. *typica* Fernald) occurred in arctic America south to Kangalaksiorvik Bay, Labrador. Malte (1934) concluded that the Kangalaksiorvik Bay specimen cited by Fernald (1924) was *A. angustata*. Upon locating the type of *A. alpina* (described from Lapland as *Gnaphalium alpinum* L.) in LINN, Malte (1934) concluded that the species did not occur in North America, at least insofar as he had not seen a North American specimen which exactly matched the type collection. Bayer (1993) supported this viewpoint, but only if a strict typological species concept were adopted. He further judged that the *A. alpina* species complex was composed of innumerable apomictic clones, and recommended a broad species circumscription until a final decision on its treatment could be reached.

Resolution of the North American occurrence question has been confounded, in part, by the green-black phyllaries shared by members of the *Antennaria alpina* and *A. media* polyploid complexes, as well as the fact that each of the complexes is phenotypically plastic. Plasticity is due in part to a preponderance of agamospermous reproduction (Holm 1920) in each of the complexes.

Several characters have been used during the past century to differentiate between *Antennaria alpina* and *A. media*. Greene (1898) noted that involucre bracts in Old World *A. alpina* are decidedly narrower and more acuminate than they are in its western American homologue *A. media*. Rydberg (1900) concluded that *A. media* differs from *A. alpina* in that the spatulate leaves of the former are conspicuously tomentose on both sides, whereas they are adaxially glabrous in the latter. Fernald (1924) added to the character suite of North American *A. alpina*, stating that the upper cauline leaves terminate in an oblong, glabrous, scarious appendage. Thus, the two main distinctions between the species are the presence of scarious tips at the ends of middle to distal peduncular leaves in *A. alpina*, these being absent in *A. media*, and the shape of involucre bracts (acute in the former and blunt in the latter). Bayer and Stebbins (1993) supported the use of these characters in their North American synopsis of the genus.

Table 4. Summary of *a posteriori* assignments and probabilities for type collections of *Antennaria*. Type collections were ultimately assigned through the use of diagnostic qualitative characters as well as the results of this analysis.

Type Collection	Type Designation	Subspecies	Probability
<i>A. alpina</i> var. <i>cana</i>	Holotype (GH)	<i>canescens</i>	0.9999
	Isotype (CAN 106057)	<i>canescens</i>	0.5088
	Paratype (GH)	<i>canescens</i>	1.0000
	Lectotype (C)	<i>canescens</i>	0.6072
	Lectotype (C)	<i>porsildii</i>	0.9997
<i>A. alpina</i> var. <i>canescens</i>	Holotype (CAN 105983)	<i>canescens</i>	0.8138
	Lectotype (CAN 105927)	<i>canescens</i>	0.8138
	Isotype (CAN 506917)	<i>canescens</i>	0.5710
	Holotype (GH)	<i>canescens</i>	1.0000
	Holotype (C)	<i>canescens</i>	0.9993
<i>A. alpina</i> var. <i>glabrata</i>	Holotype (GH)	<i>canescens</i>	1.0000
	Isotype (MT)	<i>canescens</i>	1.0000
	Paratype (MT)	<i>canescens</i>	1.0000
	Holotype (GH)	<i>canescens</i>	0.9998
	Isotype (MT)	<i>canescens</i>	0.9998
<i>A. arenicola</i>	Paratype (MT)	<i>canescens</i>	1.0000
	Paratype (MT)	<i>canescens</i>	1.0000
	Paratype (MT)	<i>canescens</i>	1.0000
	Paratype (MT)	<i>canescens</i>	1.0000
	Paratype (MT)	<i>canescens</i>	1.0000
<i>A. atriceps</i>	Paratype (MT)	<i>canescens</i>	0.9986
	Holotype (GH)	<i>canescens</i>	0.9999
	Isotype (MT)	<i>canescens</i>	0.5088
	Paratype (MT)	<i>canescens</i>	1.0000
	Paratype (MT)	<i>canescens</i>	1.0000
<i>A. brevistyla</i>	Paratype (MT)	<i>canescens</i>	1.0000
	Paratype (MT)	<i>canescens</i>	1.0000
	Paratype (MT)	<i>canescens</i>	1.0000
	Paratype (MT)	<i>canescens</i>	1.0000
	Paratype (MT)	<i>canescens</i>	1.0000
<i>A. canescens</i> f. <i>fastigiata</i>	Paratype (MT)	<i>canescens</i>	1.0000
	Paratype (MT)	<i>canescens</i>	1.0000
	Paratype (MT)	<i>canescens</i>	1.0000
	Paratype (MT)	<i>canescens</i>	1.0000
	Paratype (MT)	<i>canescens</i>	1.0000
<i>A. columnaris</i>	Paratype (MT)	<i>canescens</i>	1.0000
	Paratype (MT)	<i>canescens</i>	1.0000
	Paratype (MT)	<i>canescens</i>	1.0000
	Paratype (MT)	<i>canescens</i>	1.0000
	Paratype (MT)	<i>canescens</i>	1.0000
<i>A. confusa</i>	Paratype (MT)	<i>canescens</i>	1.0000
	Paratype (MT)	<i>canescens</i>	1.0000
	Paratype (MT)	<i>canescens</i>	1.0000
	Paratype (MT)	<i>canescens</i>	1.0000
	Paratype (MT)	<i>canescens</i>	1.0000

Table 4. Continued.

Type Collection	Type Designation	Subspecies	Probability
	Paratype (MT)	<i>canescens</i>	1.0000
	Paratype (MT)	<i>canescens</i>	1.0000
<i>A. congesta</i>	Holotype (CAN 105922)	<i>canescens</i>	1.0000
<i>A. glabrata</i> f. <i>ramosa</i>	Lectotype (CAN 281573)	<i>canescens</i>	1.0000
<i>A. longii</i>	Holotype (GH)	<i>canescens</i>	0.9969
	Paratype (GH)	<i>canescens</i>	0.9999
	Paratype (GH)	<i>canescens</i>	0.9846
	Paratype (GH)	<i>canescens</i>	1.0000
	Paratype (GH)	<i>canescens</i>	1.0000
	Paratype (GH)	<i>canescens</i>	1.0000
	Paratype (CAN 106059)	<i>canescens</i>	1.0000
<i>A. porsildii</i>	Holotype (C)	<i>porsildii</i>	0.9988
	Paratype (C)	<i>porsildii</i>	0.9994
	Paratype (C)	<i>porsildii</i>	0.9986
	Paratype (S)	<i>canescens</i>	1.0000
<i>A. somborgeri</i>	Holotype (GH)	<i>canescens</i>	0.9973
<i>A. subcanescens</i>	Holotype (CAN 106127)	<i>canescens</i>	0.9764
	Isotype (GH)	<i>alpina</i>	0.9080
<i>A. vexillifera</i>	Holotype (GH)	<i>canescens</i>	0.9998
	Isotype (MT)	<i>canescens</i>	0.7078
	Isotype (CAN 106056)	<i>canescens</i>	1.0000

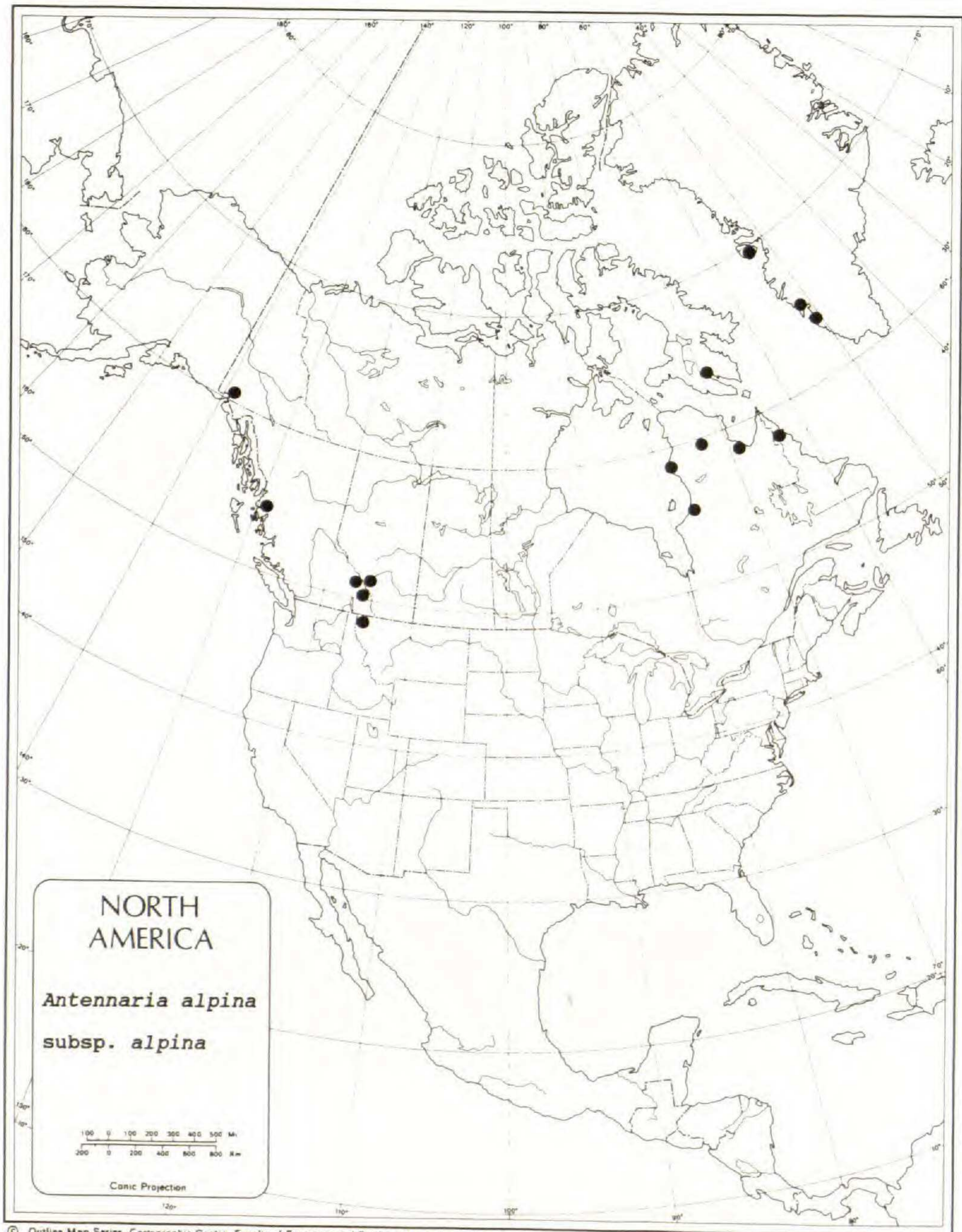
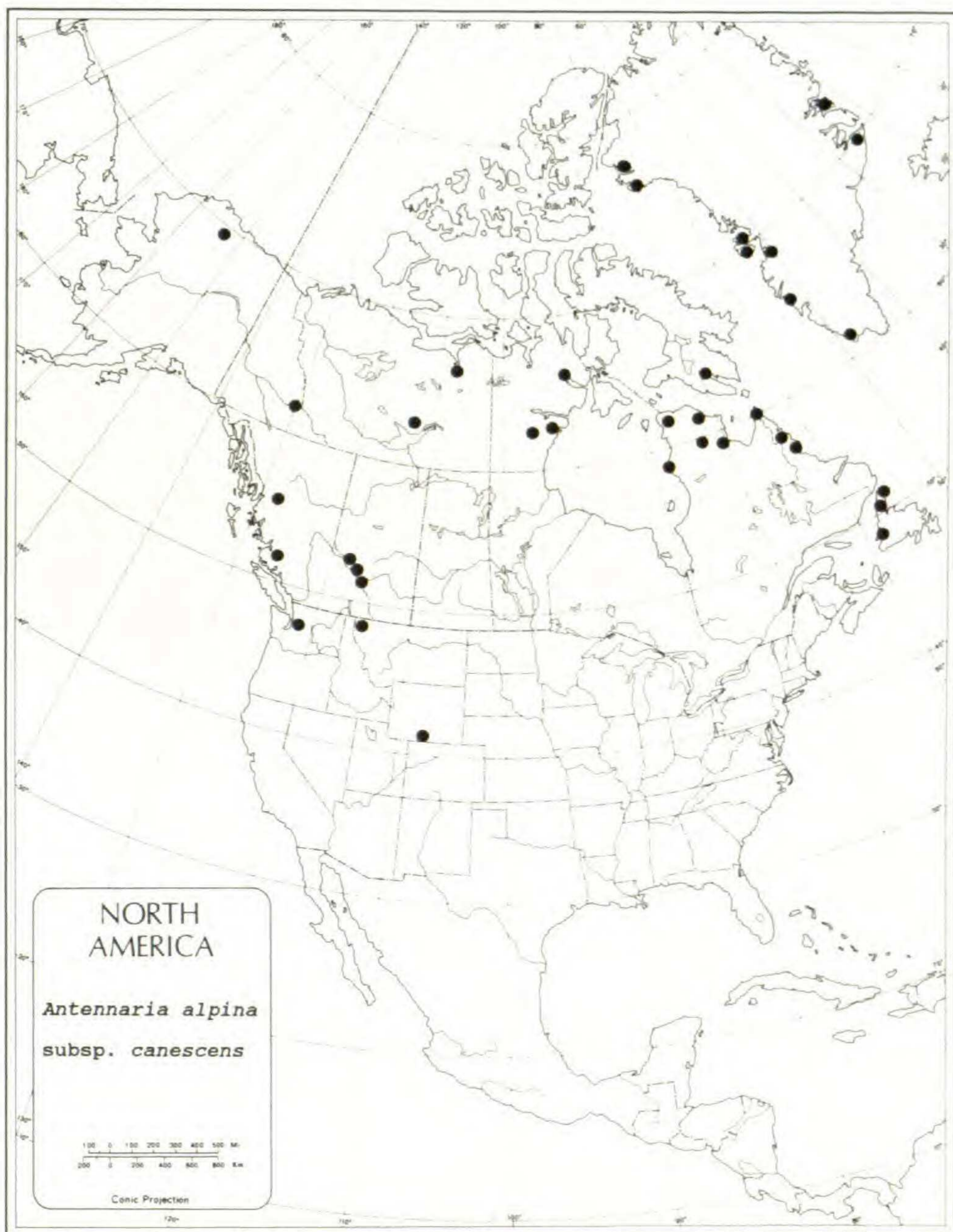


Figure 3. North American distribution of *Antennaria alpina* subsp. *alpina*. The Scandinavian distribution of the subspecies approximates that illustrated by Hultén (1968) for *A. alpina* and is therefore not presented here. Bullets may represent more than one collection.

Having now completed re-evaluations of both the *Antennaria alpina* and *A. media* (Chmielewski 1997) complexes using quantitative morphological characters, it is evident that as circumscribed here both occur in North America and their distributions



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Figure 4. North American distribution of *Antennaria alpina* subsp. *canescens*. The Scandinavian distribution of the subspecies approximates that illustrated by Hultén (1968) for *A. alpina* var. *canescens* and is therefore not presented here. Bullets may represent more than one collection.

overlap, at least partially. Further, in addition to the qualitative characters previously stated, the capitula of *A. alpina* are typically more lustrous and brighter (especially in the brown phyllaried form) than in *A. media*, and the capitulescence is typically more

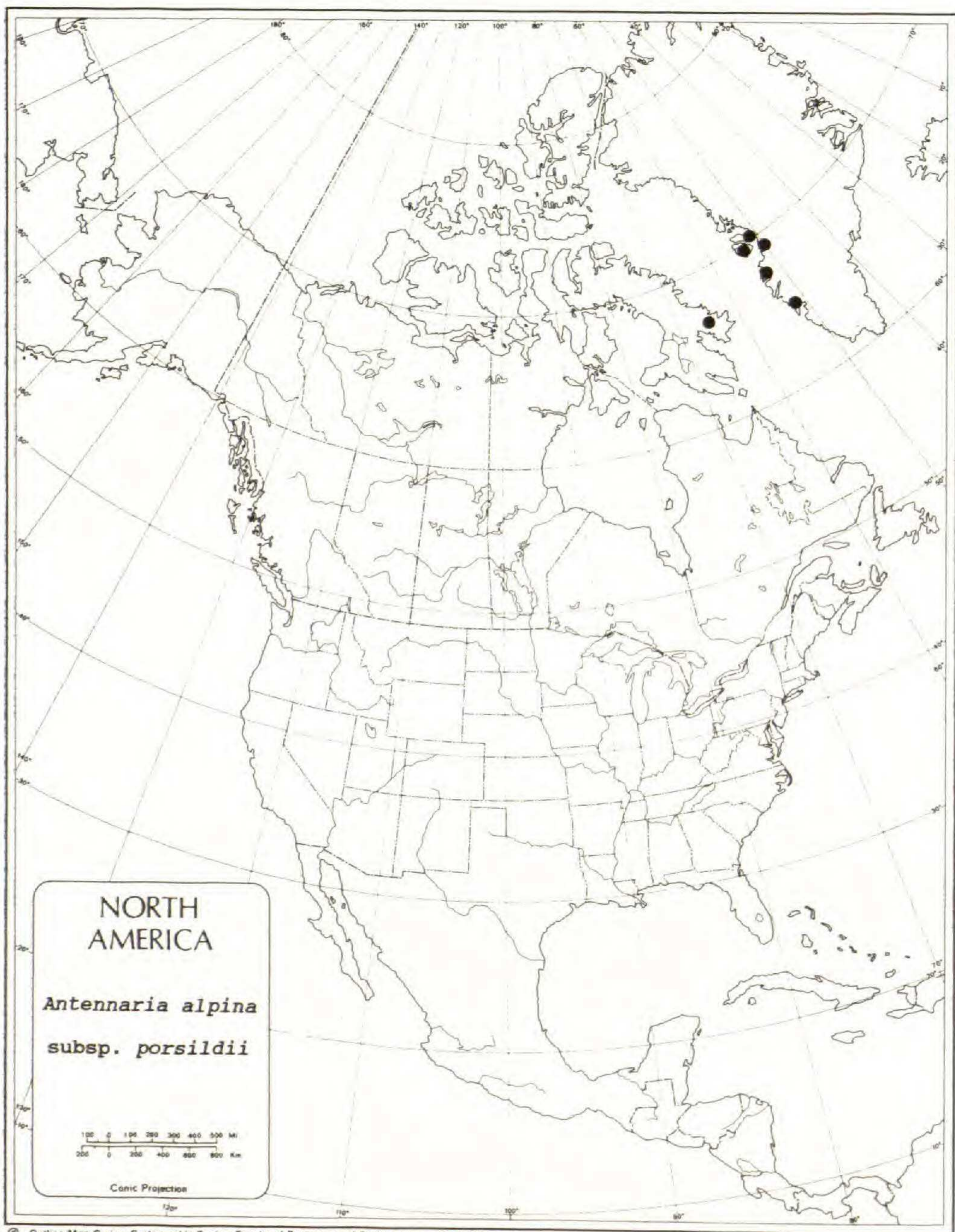


Figure 5. North American distribution of *Antennaria alpina* subsp. *porsildii*. The Greenland distribution of the subspecies approximates that presented by Böcher (1963) for *A. glabrata*. Bullets may represent more than one collection.

open in the former than in the latter. The two complexes also differ in style length, inner phyllary length, involucre length, and corolla length. The low amount of total variance (43%) explained by the first discriminant function, because of the recognition of

these two complexes, indicates that the selected quantitative characters are only somewhat useful in delimiting the complexes. Thus, the previously stated qualitative characters remain the best with which to separate members of the two complexes.

Holm (1920) noted that more or less well-marked varieties will sometimes result because of polymorphism attributable to the vast geographic distribution of species. Thus, the second data matrix was used first to assess whether patterns of geographic variation were discernible in *Antennaria alpina* and warranted infraspecific recognition, and second, to evaluate previous hypotheses relative to the colonization of Greenland by the genus.

Three characters (pappus length, style length, and involucre length) can best be used to separate Scandinavian specimens from either Greenland or North American specimens. The single misclassified (not assigned to the correct geographic group) Scandinavian specimen was assigned to the Greenland group. Distinguishing between the North American and Greenland specimens is a more difficult task, these specimens differing predominantly in basal leaf width, number of capitula, and outer phyllary width (those characters which had high loadings on the second canonical axis). Misclassified North American specimens were assigned twice as often to the Greenland than to the Scandinavian group, whereas misclassified Greenland specimens were approximately equally distributed between the geographic groups. The low amount of the total variance explained by the first discriminant function, because of the recognition of three geographic groups, indicates that the specimens should be divided on the basis of something other than geography.

R. T. Porsild (1914) regarded *Antennaria alpina* as an old species that found its way to Greenland after the glacial period, probably over Smith Sound, where the crossing may have taken place during an epoch with milder climate than now rules in Greenland. In reviewing the available literature Ekman (1927) regarded the floral immigration to Greenland to be pincer-like. That is, plants in eastern Greenland migrated from the east, presumably before the last glacial period, along an isthmus running from Scandinavia across Iceland to Greenland, whereas plants in western Greenland migrated from the northern regions of North America. A. E. Porsild (1965) opined that, in the Old World, not only was *A. alpina* endemic to the Scandinavian mountains, but that the disjunct or bicentric ranges of *A. glabrata* (J. Vahl) Greene, *A. porsildii*, and

A. ungvensis (Fernald) M. O. Malte suggested that they must have occupied at least part of their present-day range in pre-Pleistocene time. Bayer (1990b) proposed that *Antennaria* per se could have migrated to Eurasia any time from the Middle Miocene to the end of the Pleistocene. Further, he believed it more likely that the genus migrated to Eurasia via Beringia instead of across a European–North American land bridge. The occurrence of species such as *A. nordhagiana* Rune & Rønning in presumed glacial refugia in northern Norway suggested that they evolved prior to the Quaternary because they inhabited primarily unglaciated regions (Rune and Rønning 1956). Based on similarities between and among geographic groups, the results of the present study suggest that colonization of Greenland by *A. alpina* followed the pincer-like immigration proposed by Ekman (1927). It is, however, difficult to address the question of global distribution in *A. alpina* based on literature citations alone, as distribution is intimately tied to the manner in which the taxon was delimited by the respective author(s).

The third set of analyses dealt specifically with the delimitation of infraspecific taxa within *Antennaria alpina*. Although numerous infraspecific taxa were previously proposed for *A. alpina*, the results of this study support the recognition of only three. In keeping with the criteria utilized in recent revisions of the genus (e.g., Bayer 1990a; Bayer and Stebbins 1982; Chmielewski 1993, 1994a, b, 1995a, b, 1997; Chmielewski and Chinnappa 1988a, 1991) the following subspecies are recognized: *A. alpina* subsp. *alpina*, *A. alpina* subsp. *canescens* (Lange) Chmielewski, and *A. alpina* subsp. *porsildii* (E. Ekman) Chmielewski.

Both qualitative and quantitative characters may be used, in part, to distinguish among the three subspecies, but the former are unquestionably the better. Qualitative characters include: (1) the degree to which stoloniferous growth has developed and (2) whether the basal leaf surfaces are glabrous or not. Stolons are short and leafy in subsp. *porsildii*, are variable in subsp. *canescens*, but generally well developed, and are well developed in subsp. *alpina*. The basal leaves of subsp. *alpina* are bright green and glabrous or glabrate adaxially and villous or tomentose abaxially. The basal leaves of subsp. *canescens* are permanently villous-tomentose both adaxially and abaxially. In subsp. *porsildii* the entire plant, including both surfaces of the basal leaves, is glabrous.

Quantitative characters which can best be used to distinguish between and among the subspecies were summarized previously. Some of these characters, such as peduncle length, number of peduncular leaves, and number of capitula, are more sensitive to environmental cues than are the strictly reproductive characters of the florets. Plasticity in response to environmental factors, as well as polyploidization, undoubtedly reduces the usefulness of some of these characters for separation of the subspecies. Despite their differences, the quantitative characters do tend to exhibit greater uniformity between and among subspecies than occurs with the qualitative characters.

Analysis of the third data matrix also allowed for the *a posteriori* assignment of type collections of several taxa to one of the subspecies adopted here. Except for the assignment of *Antennaria brevistyla* and *A. glabrata* f. *tomentosa*, this treatment is in agreement with that proposed by Bayer and Stebbins (1993) for the listed taxa, insofar as they both support their inclusion in *A. alpina*. Bayer and Stebbins (1993) tentatively assigned *A. brevistyla* to *A. rosea* Greene subsp. *confinis* (Greene) R. Bayer, whereas I assign the species to subsp. *canescens*. *Antennaria glabrata* f. *tomentosa* E. Ekman (= *A. hudsonica* M. O. Malte) is included here as part of subsp. *canescens*, but was previously assigned to *A. monocephala* subsp. *angustata* (Greene) Hultén (Bayer and Stebbins 1993; Chmielewski and Chinnappa 1991). Disagreement between the present study and the synopsis for the genus presented by Bayer and Stebbins (1993) occurs predominantly among those species which were not included as part of this study (*A. bayardi* Fernald, *A. brunnescens* Fernald, *A. compacta* M. O. Malte, *A. foggii* Fernald, *A. pallida* E. Nelson, *A. pedunculata* A. E. Porsild, *A. rousseaui* A. E. Porsild, and *A. stolonifera* A. E. Porsild) because they were previously assigned to other taxa (see Chmielewski 1995a, b, 1997). Further, Bayer and Stebbins (1993) also included *A. intermedia* (Rosenv.) A. E. Porsild and *A. wiegandii* Fernald in synonymy with *A. alpina*, whereas it is my opinion that the former should be included within *A. pallida* (Chmielewski 1995a) and the latter within *A. howellii* Greene subsp. *gaspensis* (Fernald) Chmielewski (Chmielewski 1995b).

Antennaria alpina is essentially a gynoecious species. The staminate plant was previously reported as being exceedingly rare, having been found only a few times in France, Scandinavia, and

Alaska (Holm 1920) and more recently in the Canadian Yukon Territory (Bayer 1993). The occurrence of staminate specimens of *A. alpina* from France seems unlikely since the species does not appear to occur there (Bayer and Stebbins 1987; Hultén 1968). These species distributions suggest that the reports are for staminate *A. dioica* and not *A. alpina*. Because staminate specimens of *A. alpina* were reported to occur only in association with *A. dioica* in Scandinavia (Ekman 1927), it also seems reasonable to question whether they were simply misidentified as belonging to the former species when in reality they belonged to the latter. However, Nygren (1950) did conclude that in some areas of the Scandinavian mountains (in the Paldsa area) staminate plants are not rare. The Alaskan specimens to which Holm (1920) refers could reasonably be either *A. monocephala* subsp. *monocephala* or *A. frieseana* (Trautv.) Ekman subsp. *alaskana* (M. O. Malte) Hultén, as reference is made to each as being part of *A. alpina*. Finally, the staminate specimen cited as *A. alpina* by Bayer (1993) from the Yukon Territory was treated as *A. media* subsp. *media* by Chmielewski (1997). Staminate plants have not been reported from either northeastern Canada (Porsild 1965) or Greenland (Ekman 1927; Porsild 1965). Not having seen any staminate specimens of *A. alpina* among the thousands examined during the course of this investigation, I tend to believe that they do not exist.

Asexual reproduction in *Antennaria alpina* occurs either through the production of vegetative offsets or through agamospermy. Viable seeds apparently are produced in abundance (Holm 1920). This apomict may, however, give rise to staminate plants via chromosome segregation (Bayer and Stebbins 1987). The staminate plants could, in turn, then pollinate pistillate plants if the two come into contact. The lack of functional pollen (Porsild 1965) in presumed staminate specimens of *A. alpina* does, however, negate the possibility of fertilization.

Polyploid agamic complexes such as *Antennaria alpina* have evolved through hybridization events between and among sexual species. Several hypotheses have been put forth relative to the origin of the complex, including: (1) derivation from *A. dioica* (Rune and Rønning 1956); (2) hybridization among the diploids *A. aromatica* Evert, *A. densifolia* A. E. Porsild, *A. frieseana* subsp. *alaskana*, *A. media*, *A. monocephala*, and *A. nordhagiana* (Bayer 1987); and (3) hybridization among *A. aromatica*, *A. frie-*

seana subsp. *alaskana*, *A. media*, *A. monocephala*, and *A. nordhagiana* (Bayer and Stebbins 1987). I believe the *A. alpina* polyploid complex is rooted in hybridization events between *A. dioica* and *A. frieseana* subsp. *alaskana*.

R. T. Porsild (1914) concluded that *Antennaria alpina* was an old species, and that *A. glabrata* was a young species that developed from it. The distribution of *A. glabrata*, *A. porsildii*, and *A. ungavensis* led A. E. Porsild (1965) to conclude that they were not of recent hybrid origin, at least pre-Pleistocene time. Bayer (1990b) stated that polyploid agamic complexes such as *A. alpina* were the most recent to evolve because they were derived from the sexual progenitors of section *Catipes*. I agree with the statement of Rune and Rønning (1956) that *A. nordhagiana* and *A. porsildii* are parallel derivatives (both being glabrous) from *A. dioica* and *A. alpina*, respectively.

In summary, not only does *Antennaria alpina* s.l. occur in North America, but so do its three subspecies. The best characters to use to distinguish among the subspecies are the degree and distribution of pubescence on the surfaces of the basal leaves (see key). In subsp. *alpina* the leaves are glabrous on the adaxial surface and villous or tomentose on the abaxial; in subsp. *canescens* the leaves are villous or tomentose on both surfaces; in subsp. *porsildii* the leaves are entirely glabrous.

TAXONOMIC TREATMENT

1. Plants with well-developed, prostrate or ascending stolons, abaxial surface of basal leaves villous-tomentose (2)
 2. Basal leaves glabrous on the adaxial surface
 1. *A. alpina* subsp. *alpina*
 2. Basal leaves villous-tomentose on the adaxial surface
 2. *A. alpina* subsp. *canescens*
 1. Plants with poorly developed, erect or suberect stolons, abaxial surface of basal leaves glabrous
 3. *A. alpina* subsp. *porsildii*

1. ***Antennaria alpina*** (L.) Gaertner subsp. ***alpina***, De Fruct. Sem. Pl. 2: 410. 1791.

Gnaphalium alpinum L., Sp. Pl. 850. 1753. *Antennaria alpina* var. *typica* Fernald, Rhodora 26: 98. 1924; BASIONYM: *Gnaphalium alpinum*. TYPE: LAPLAND. No. 71—see Malte (1934) for discussion on this typification (LINN—microfiche!).

Antennaria alpina (L.) Gaertner var. *ungavensis* Fernald, *Rhodora* 18: 238. 1916. *A. ungvensis* (Fernald) M. O. Malte, *Rhodora* 36: 110. 1934; TYPE: CANADA. Ungava (Labrador): Stillwater River, 12 Aug 1896, *Spreadborough Geol. Surv. Can. no. 44442* (HOLOTYPE: GH!; ISOTYPE: CAN 105999!).

Antennaria arenicola M. O. Malte, *Rhodora* 36: 110. 1934. TYPE: CANADA. Quebec: east coast of Hudson Bay, Port Harrison, 58°17'N, 78°10'W, 18–20 Aug 1928, *Malte 120714* (HOLOTYPE: CAN 105983!; ISOTYPE: CAN 105982!).

Humifuse; stolons usually obvious, up to 10 cm long; basal leaves spatulate-oblongate, green, glabrous adaxially and villos-tomentose abaxially, 10–16 mm long, 2–4 mm wide; peduncle typically <18 cm long, bearing 7–12 peduncular leaves, middlemost 11–19 mm long, 1.4–2.4 mm wide, middle to distal tipped with a flat, oblong, scarious appendage; capitula 3–7 in corymb, 5–7 (8) mm long; phyllaries narrow, linear-lanceolate, acute, green, brown, black, or olivaceous, outermost 3–5 mm long, 0.9–1.3 mm wide, innermost longer, comparatively narrower, 5–6.4 mm long, 0.6–0.8 mm wide; corolla 3.5–4.7 (5) mm long; style 4.3–5.7 mm long; pappus bristles 4.6–6.2 mm long; cypselae brown, commonly glabrous, occasionally papillate, 0.7–1.6 mm long. Chromosome number determinations reported for the species (some under synonyms) from North America and Europe range between $2n = 56$ and 112 (Bayer 1984, 1990a; Bayer and Stebbins 1981, 1987; Chinnappa 1986; Chmielewski and Chinnappa 1988b, c, 1990; Halliday 1976; Lid 1963, as cited in Porsild 1965). Unless the actual specimen for which a chromosome number determination has been made is available for viewing, determinations as they pertain to specific taxa should, however, be considered with caution (i.e., I don't know which, if any, of the reports are from specimens belonging to my circumscription of subsp. *alpina*).

DISTRIBUTION AND HABITAT. *Antennaria alpina* subsp. *alpina* occurs on gravel, shale, or talus slopes, rocky schist cliffs, and wet or dry meadows to the alpine zone in western and eastern North America, Greenland, Scandinavia, and possibly to northwest Russia (Figure 3).

REPRESENTATIVE SPECIMENS: **Canada.** ALBERTA: Banff National Park, Sulphur Mtn., 22 Jul 1891, *Macoun 73013* (CAN); BRITISH COLUMBIA: Paradise Mine, ca. 15 mi west of Windermere, 31 Jul 1953, *Calder & Savile 11262*

(DAO); LABRADOR: Torngat Region, Kikkertasoak Island, Saglek Bay, 9 Aug 1926, *Woodworth 412* (CAN); NORTHWEST TERRITORIES: Franklin District, Baffin Island, Frobisher Bay, Ogac Lake, head of Ney Harbour, 5 Aug 1965 *McLaren 79* (CAN); QUEBEC: Fort Chimo, 11 Jul 1948, *Rousseau 44* (CAN).

Greenland. Godtchaab District, Ameralik Fjord, 64°07'N and 51°08'W, 20 Jul 1941, *Porsild 8200* (CAN).

Norway. Slopes of Oksfjellet east side of Tverelva River, 20 Jul 1968, *Alho & Kause* (DAO).

Sweden. Torne Lappmark, Karsovagge Valley, 17 Jun 1957, *Ray 26* (DAO); near Bjorkliden, 29 Jul 1950, *Moldenke & Moldenke 21046* (DAO).

2. *Antennaria alpina* (L.) Gaertner subsp. **canescens** (Lange) Chmielewski *comb. et stat. nov.*

Antennaria alpina var. *canescens* Lange, *Flora Danica XLVII*. tab. 2786, fig. 1. 1869. *A. canescens* (Lange) M. O. Malte, *Rhodora* 36: 109. 1934. *A. canescens* subsp. *canescens* [autonym generated by *A. canescens* subsp. *porsildii* (E. Ekman) Löve and Löve, *Bot. Not.* 128: 519. 1976]. In principle, the plants depicted in *Flora Danica* tab. 2786 were drawn in nature. Thus, the drawings are the type specimens, and consequently none were cited in the protologue. In C is a sheet which includes three collections numbered 1, 2, 3. The specimen designated as number 3 bears a striking resemblance to the type drawing and in my estimation is one and the same. TYPE: GREENLAND. District Colon. Godthaab: Jul–Aug, *Vahl s.n.* (LECTOTYPE: C!—here designated).

Antennaria canescens f. *fastigiata* Böcher, *Arbejd. Dansk. Arkt. Sta. Disko* 38: 33. 1963. TYPE: GREENLAND. Holsteinsborg (Mount Praestefjeldet), 66°56'N and 53°40'W, 18 Jul 1958, *Böcher 623* (HOLOTYPE: C!).

Antennaria alpina var. *cana* Fernald & Wiegand, *Rhodora* 13: 24. 1911. *A. cana* (Fernald & Wiegand) Fernald, *Rhodora* 18: 236. 1916. TYPE: CANADA. Newfoundland: Pointe Riche, 4 Aug 1910, *Fernald & Wiegand 4139* (HOLOTYPE: GH!; ISOTYPE: CAN 106057!).

Antennaria sornborgeri Fernald, *Rhodora* 18: 237. 1916. TYPE: CANADA. Labrador: Rama, 20–24 Aug 1897, *Sornborger 156* (HOLOTYPE: GH!).

Antennaria vexillifera Fernald, *Rhodora* 26: 99. 1924. TYPE: CANADA. Quebec: Matane County, between Mt. Mattaouisse and Mt. Collins, 8 Jul 1923, *Fernald, Griscom, Mackenzie, Pease, & Smith 26056* (HOLOTYPE: GH!; ISOTYPES: MT!, CAN 106056!).

Antennaria alpina f. *latifolia* E. Ekman, *Svensk Bot. Tidskr.* 21: 50. 1927. TYPE: GREENLAND. Umanak, 25–30 Aug 1923, *Ekman s.n.* (LECTOTYPE: S!—here designated).

Antennaria glabrata (J. Vahl) Greene f. *tomentosa* E. Ekman, *Svensk Bot. Tidskr.* 21: 51, pl. 1, figs. 3, 9. 1927. *A. hudsonica* M. O. Malte, *Rhodora* 36: 116. 1934. TYPE: GREENLAND. Narssak near Nord-Pröven, ca. 72°23'N. Type collections cited to be at C could not be located (Fredskild, pers. comm.). Inclusion of this form in

subsp. *canescens* is based on the description which indicates that the rosette leaves are lanate-tomentose abaxially.

- Antennaria longii* Fernald, *Rhodora* 28: 237. 1927. TYPE: CANADA. Newfoundland: Pistolet Bay, Schooner (Brandy) Island, 18 Jul 1925, *Pease & Long 29177* (HOLOTYPE: GH!).
- Antennaria brevistyla* Fernald, *Rhodora* 33: 323. 1931. TYPE: GREENLAND. S. Disko, Nuk ost for Marraq, 69°25'N, 13 Aug 1929, *Porsild s.n.* (HOLOTYPE: GH!; ISOTYPE: CAN 450374!).
- Antennaria columnaris* Fernald, *Rhodora* 35: 331. 1933. TYPE: CANADA. Newfoundland: Gargamelle Cove, 20 Jul 1929, *Fernald, Long, & Fogg, Jr. 2076* (HOLOTYPE: GH!; ISOTYPE: MT!).
- Antennaria confusa* Fernald, *Rhodora* 35: 338. 1933. TYPE: CANADA. Newfoundland: Old Port au Choix, 21 Jul 1929, *Fernald, Long, & Fogg, Jr. 2078* (HOLOTYPE: GH!; ISOTYPE: MT!).
- Antennaria atriceps* Fernald ex Raup, *Contr. Arnold Arb.* 6: 207, pl. 8, fig. 2. 1934. TYPE: CANADA. British Columbia: west and northwest slopes of Mt. Selwyn, 56°1'N and 123°39'W, near small lake, elevation 5000 ft, 26 Jul 1932, *Raup & Abbe 4134* (LECTOTYPE: CAN 105927!—here designated; ISOLECTOTYPE: CAN 506917!).
- Antennaria congesta* M. O. Malte, *Rhodora* 36: 114. 1934. TYPE: CANADA. Quebec: Port Burwell, Hudson Strait, 60°22'N and 64°50'W, 25–28 Jul 1928, *Malte 120118* (HOLOTYPE: CAN 105922!). This name was previously placed in synonymy with *A. monocephala* subsp. *angustata* (Chmielewski and Chinnappa 1991).
- Antennaria subcanescens* Ostenfeld ex M. O. Malte, *Rhodora* 36: 112. 1934. TYPE: CANADA. Northwest Territories: Mackenzie District, Bernard Harbour, 68°47'N and 114°46'W, 14 Aug 1915, *Johansen 91546* (HOLOTYPE: CAN 106127!; ISOTYPE: GH!).
- Antennaria canescens* var. *pseudoporsildii* Böcher, *Meddel. Gronl.* 148(3): 32, fig. 9. 1963. *A. boecheriana* A. E. Porsild, *Bot. Tidsskr.* 61: 36. 1965. TYPE: GREENLAND. Kangerdlvarssuk Ikamiut, 65°48'N, 1958, *Böcher 270*. Although the type collection was cited as being in C it could not be located (Fredskild, pers. comm.). Because new rosette leaves of var. *pseudoporsildii* are initially hairy (these are lost with age), the taxon is included in subsp. *canescens*.

Stolons well developed, prostrate or ascending, up to 10 cm long; basal leaves spatulate-oblongate, permanently whitened both adaxially and abaxially with a silvery tomentum, 7–15 mm long, 2–4 mm wide; peduncle typically <12 cm long, bearing up to 10 linear peduncular leaves, middlemost 8–14 mm long, 1–2 mm wide, middle to distal tipped with a flat, oblong, scarious appendage; capitula 3–6 in corymb, 5–6.4 mm long; phyllaries linear-lanceolate, acute, green-black tipped, outermost 3–5 mm long, 0.8–1.4 mm wide, innermost longer, comparatively narrower, 4.8–6 mm long, 0.5–0.9 mm wide; corolla 3.2–4.2 mm long;

style 3.8–5.0 mm long; pappus bristles 4.5–5.5 mm long; cypselae brown, not papillate, 0.7–1.4 mm long. Chromosome number determinations for Greenland populations of $2n = 63$ (Jorgensen et al. 1958) are supplemented with North American $2n = 56$ (Chmielewski 1995c) and $2n = 70$ (Chmielewski and Chinnappa 1988d) counts.

DISTRIBUTION AND HABITAT. *Antennaria alpina* subsp. *canescens* occurs on various substrates, including granitic outcrops, gravel river beds, limestone gravel beds, and sand embankments in Scandinavia, coastal Greenland, Labrador, the Hudson Bay region, southern Baffin Island, west through the Canadian and Alaskan Arctic and south through the Rocky Mountains to Wyoming (Figure 4).

REPRESENTATIVE SPECIMENS: **Canada.** ALBERTA: Jasper National Park, near summit of Mt. Edith Cavell trail, 4 Aug 1989, *Chmielewski & Chmielewski* CC4889 (UAC)—Note: Collections CC2135, CC2136, and CC2717 reported by Chmielewski and Chinnappa (1988b) as *A. stolonifera* A. E. Porsild better represent subsp. *canescens* and are treated as such here; LABRADOR: Crater Lake, North Hebron River valley, ca. 52 mi west southwest of Hebron, 58°02'N and 64°02'W, 26 Jul 1954, *Gillett* 8648 (DAO); NEWFOUNDLAND: Region of St. John Bay, Eastern Point, 26 Jul 1919, *Fernald, Long, & Fogg, Jr.* 2085 (MT); NORTHWEST TERRITORIES: Franklin District, Baffin Island, Frobisher Bay, Ogac Lake, 15 Aug 1962, *McLaren* 7 (CAN); Keewatin District, Yathkyed or Hicolikdjuak Lake on the Kazan River, 62°30'N and 97°–98°30'W, 1–15 Aug 1930, *Porsild* 5854 (CAN); Mackenzie District, Desperation Lake, 62°35'N and 112°15'W, 8 Jul 1961, *Scotter* 1051 (DAO); QUEBEC: Wakeman Bay, 60°N and 70°W, Aug 1937, *Dutilly* 4016 (CM); YUKON TERRITORY: Itsi Range, unnamed lake, 62°57'N and 130°09'W, 31 Jul–2 Aug 1960, *Calder & Kukkonen* 27655 (DAO).

Greenland. Nugsuak Peninsula, Kingigtok, 70°10'N, 21 Jul 1928, *Erlanson* 3288 (DAO).

Norway. Dovre, Opland, Fokstuen, 23 Jun 1939, *Osterlind* (DAO).

Sweden. Lapland, Tornetrask District, Jukkasjarvi Parish, Mt. Paddos, 68°–68°34'N and 18°–20°30'E, 12 Jul 1952, *Alm* 1508 (DAO).

United States. ALASKA: 3 mi north of Okpilak Lake, 69°27'N and 153°58'W, 26 Jul 1958, *Cantlon & Malcolm* 58-0391 (CAN); MONTANA: Flathead County, Glacier National Park, southeast of Gem Lake, 4 Aug 1987, *Lesica* 4469 (MONTU); WASHINGTON: Whatcom County, Chowder Ridge, 7 mi southeast of Glacier, 31 Jul 1972, *Douglas & Douglas* 4289 (DAO); WYOMING: Carbon County, Medicine Bow Range, between Lake Marie and Silver Lake, 5 Aug 1966, *Porter & Porter* 10268 (CAS).

3. *Antennaria alpina* (L.) Gaertner subsp. *porsildii* (E. Ekman)
Chmielewski *comb. nov.*

- Antennaria porsildii* E. Ekman, Svensk Bot. Tidskr. 21: 51, pl. 1, figs. 10, 11. 1927. *A. alpina* var. *porsildii* Sorensen, Meddel. Gronl. 101(3): 89. 1933. *A. canescens* (Lange) M. O. Malte subsp. *porsildii* (E. Ekman) Löve & Löve, Bot. Not. 128: 519. 1976. TYPE: GREENLAND. Danmarks Insel, ca. 70°30'N, Aug 1892, Hartz s.n. (HOLOTYPE: C!).
- Antennaria alpina* var. *glabrata* J. Vahl, Flora Danica XLVII. tab. 2786, fig. 4. 1869. *A. glabrata* (J. Vahl) Greene, Pittonia 3: 285. 1898. In principle, the plants depicted in Flora Danica tab. 2786 were drawn in nature. Thus, the drawings are the type specimens, and consequently none were cited in the protologue. In C is a sheet which at one time presumably consisted of two collections. Collection number 1 is missing, but collection number 2 bears a striking resemblance to the type drawing but is not exactly the same. The type drawing has three capitula and five roots, whereas the specimen per se has only two capitula and no obvious roots. I suspect that these have been lost as a consequence of handling. Further, the collection from insula Disco is labelled Dette Expl. Benyttet til Flora Danica (this specimen used for Flora Danica). TYPE: GREENLAND. Disco, Jul–Aug, Vahl s.n. (LECTOTYPE: C!—here designated).
- Antennaria glabrata* f. *ramosa* A. E. Porsild, Meddel. Gronl. 58: 181. 1926. TYPE: GREENLAND. Patut, 70°14'N, 8 Aug 1921, Porsild s.n. The type collection believed to be at C could not be located (Fredskild, pers. comm.). However, a single collection in CAN fits the protologue. (LECTOTYPE: CAN 281573!—here designated).
- Antennaria porsildii* f. *roseola* E. Ekman, Svensk Bot. Tidskr. 21: 52. 1927. TYPE: GREENLAND (presumably, as no specimen was cited). This form presumably differs from subsp. *porsildii* only in its pale red versus olivaceous-brown phyllaries.

Stolons short, suberect; basal leaves spathulate-linear or oblanceolate, glabrous, 9–16.5 mm long, 2–3 mm wide; peduncle slender, 4–8 cm long, bearing 4–8 linear peduncular leaves, middlemost 10–13.5 mm long and 1.2–1.8 mm wide, middle to distal tipped with a flat, oblong, scarious appendage; 1 or 2–4 capitula, 5.5–6.7 mm long; phyllaries oblong-lanceolate, acute, green-black tipped, outermost 4–5.5 mm long, 1–1.5 mm wide, innermost longer, comparatively narrower, 5.4–6.5 mm long, 0.7–0.9 mm wide; corolla 3.8–5.8 mm long; style 4.2–5.0 mm long; pappus 5.0–5.8 mm long; cypselae brown, not papillate, 0.9–1.3 mm long. Chromosome number determinations for Greenland and Scandinavian specimens (as *A. porsildii*) included $2n = 63$, 84 (Böcher 1950; Jorgensen et al. 1958) and $2n = 63$ (Nygren 1950; Lid 1963), respectively.

DISTRIBUTION AND HABITAT. *Antennaria alpina* subsp. *porsildii* occurs in dry rocky places among grasses or on fertile slopes at lower elevations (<700 m) in western Greenland as well as eastern arctic Canada (Figure 5).

REPRESENTATIVE SPECIMENS: **Canada.** NORTHWEST TERRITORIES: Franklin District, Baffin Island, Cape Searle, 67°10'N and 62°30'W, 16–17 Aug 1950, *Wynne-Edwards 9146* (CAN).

Greenland. Arveprinsens Ejland, Kangerdlo, northeast of Ata, 69°47'N, 50°52'W, 3 Aug 1981, *Fredskild 489* (DAO); Disko, Artisk Station, 69°15'N, 31 Aug 1925, *Porsild s.n.* (GH); Svartenhuk Halvo, Umivik, 71°38'N, 18 Jul 1929, *Porsild & Porsild s.n.* (GH); Ameragdla, northwest of Kilaersarfik, 18 Jul 1984, *Fredskild 84-115* (DAO); Isortoq, Holsteinsborg, Aug 1832, *J. Vahl s.n.* (C).

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